

THE GENERA OF PONTEDERIACEAE IN THE
SOUTHEASTERN UNITED STATES¹THOMAS J. ROSATTI²PONTEDERIACEAE Kunth in Humboldt, Bonpland, & Kunth, *Nova Gen. Sp. Pl.* 1: 211 (folio ed.); 265 (quarto ed.). 1816, "Pontedereae," nom. cons.

(PICKEREL-WEED FAMILY, WATER-HYACINTH FAMILY)

Submersed, emersed, or floating aquatic herbs, sometimes on wet ground because of lowered water levels. Stems sympodial, successive axes terminating in inflorescences, stout or elongate. Juvenile leaves, especially if submersed, usually sessile and linear. Adult leaves simple, alternate [or whorled in *Hydrothrix*]; stipulate or exstipulate; the bases mostly sheathing, either open or fused basally around the stem; sessile or petiolate, the petioles sometimes inflated; the blades linear [filiform in *Hydrothrix*] to orbicular, sometimes sagittate or cordate, the veins parallel, usually arching. Inflorescence a terminal spike, raceme, panicle, or single flowered; sessile or pedunculate, subtended and enclosed to various degrees by a sheathing bract that is sometimes surmounted by a variously reduced petiole and/or blade, each flowering stem (i.e., that which is not part of the sympodium) also bearing a single leaf that some-

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The illustration of *Pontederia* was drawn in 1956 and 1957 by Dorothy H. Marsh from living materials collected by Carroll Wood and Richard J. Eaton and dissected by Wood.

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times differs from the others. Flowers perfect (some species of *Eichhornia* and *Pontederia* tristylous); perianth petaloid, biseriate, usually funnelform to salverform [parts nearly distinct in *Monochoria*], zygomorphic, subactinomorphic, or actinomorphic, the 6 [4, rarely 3, in *Scholleropsis*] lobes imbricate, often unequal. Stamens usually 6 (in 2 series of 3) or 3 [4 in *Scholleropsis*], 1 in some cleistogamous flowers [and in *Hydrothrix*], staminodes sometimes present when stamens fewer than 6; filaments inserted on the perianth tube at various levels; anthers held at various levels, basifixed, auriculate and somewhat movable on filaments (and therefore appearing dorsifixed), bilocular, with introrse, longitudinal dehiscence [rarely terminal pores]; pollen bi- or trinucleate when shed, with 1 to 3 distal or subequatorial colpi. Gynoecium of 3 united carpels; style single, of various lengths (i.e., some species tristylous); stigma terminal, entire or variously toothed and/or lobed (often 3- or 6-parted); ovary superior, with 3 locules, each locule with an axile placenta, or with 1 locule and 3 intrusive parietal placentae, or with 1 locule (through abortion of 2 locules) and a terminal placenta (in *Pontederia*); ovules in each locule numerous (solitary in *Pontederia*), anatropous, crassinucellar, and bitegmic; nectaries septal (lacking in *Heteranthera*). Fruit a many-seeded, loculicidal capsule or a 1-seeded utricle (in *Pontederia*). Seeds small, ovoid, at least those in capsules with longitudinal ridges or ribs; endosperm starchy; embryo axile, cylindrical, with a terminal cotyledon and a lateral plumule. (Including *Heterantheraceae* J. G. Agardh, *Theoria Syst. Pl.* 36. 1858, "Heteranthereae.")
TYPE GENUS: *Pontederia* L.

A small family of fresh-water aquatics comprising about six genera and 30 species, mostly pantropical but extending into the temperate zones as well. Although of diverse habit (submersed, emersed, or free floating; erect or prostrate; rhizomatous, stoloniferous, or neither), the plants are all more or less obviously sympodial in structure: each successive axis terminates in an inflorescence that may appear to be axillary.

Plants in the family are most readily distinguished by a combination of characters, including (in addition to the sympodial structure) herbaceous stems enveloped to various extents by sheathing leaf bases; inflorescences subtended by a single sheathing bract; usually six petaloid, nongreen tepals in two series of three, variously connate basally; stamens adnate to the perianth; and superior ovaries.

Three tribes, each represented in the Southeast, were recognized in the *Pontederiaceae* by Schwartz (1927, 1930). Although both the *Eichhornieae* Schwartz and the *Heteranthereae* Schwartz have three-locular ovaries (appearing one-locular at maturity in *Hydrothrix* Hooker f.) and many-seeded capsules, the *Pontederieae* (*Pontederia* L. and *Reussia* Endl.) have a single fertile locule and a one-seeded, indehiscent fruit. Mostly funnelform perianths and six stamens characterize the monogeneric *Eichhornieae*; flowers in the *Heteranthereae* normally have either mostly salverform perianths and three or fewer stamens (*Heteranthera* Ruiz & Pavón, with three stamens of two more or less distinct kinds; *Scholleropsis* H. Perr., with three stamens of two kinds; and *Hydrothrix*, with one stamen and two staminodes) or initially campanulate but ultimately

spreading to almost rotate perianths of nearly separate tepals and six stamens (*Monochoria* Presl). Extraregional genera of Heteranthereae include *Scholleropsis* (one species in Madagascar with four or rarely three tepals), *Hydrothrix* (one or two Brazilian species with filiform leaves), and *Monochoria* (perhaps five species ranging from northeastern Africa to Manchuria, Japan, and Australia; one of these established in experimental rice plots in California, according to Mason). The monotypic genera *Eurystemon* E. J. Alex. (Texas and northern Mexico) and *Zosterella* J. K. Small (widely distributed in Mexico and North America) are included here in *Heteranthera*. *Reussia* (two or three species in South America) is treated as a subgenus of *Pontederia*.

The systematic position of the Pontederiaceae has long been a subject of controversy. The group is considered by many to be most closely related to the Philydraceae (e.g., Casper & Krausch, Dahlgren & Clifford, and Thorne) and/or the Haemodoraceae (e.g., Cronquist; Dahlgren; Simpson, in press) and has been variously allied at higher levels with, among other families, the Bromeliaceae and/or Commelinaceae by some and the Liliaceae by others.

In Thorne's system the Pontederiineae (Pontederiaceae and Philydraceae) were included as one of seven suborders in the Commelinales; the Commeliniflorae and the Liliiflorae were placed as far apart as possible among the five superorders of monocotyledons recognized. Thorne further proposed (p. 100) that the Pontederiineae and Bromeliineae share a "rather close common origin" and thought that misplacement of the former with groups included in his Liliiflorae was probably due to the presence in the Pontederiineae of a petaloid (although biseriate) perianth that is often connate at the base and mostly zygomorphic, as well as to a cylindrical embryo centrally placed in abundant, starchy endosperm. Castellanos, on the other hand, considered the Pontederiaceae to be related to the Commelinaceae because both exhibit zygomorphy and androecial reduction. On the basis of starch grains, Czaja recognized three groups of monocots, one including the Bromeliaceae, Commelinaceae, Haemodoraceae, Philydraceae, and Pontederiaceae, and another the Liliaceae and their close relatives. Likewise, Huber suggested that the superorder Pontederiiflorae (Pontederiales and Philydrales) had more in common with the Bromeliiflorae, Haemodoriflorae, and Commeliniflorae than with the Liliiflorae.

A number of systematists have considered the Pontederiaceae to be more closely allied to the Liliaceae than to either the Bromeliaceae or the Commelinaceae. Although Bentham (in Bentham & Hooker) thought that the flowers indicated a close relationship with the Liliaceae, Baillon and Solms-Laubach (1883a) were among the first to suggest unification with that family. Such a proposal was later at least tacitly accepted by Schwartz (1930), who nevertheless considered the floral zygomorphy, androecial reduction, and mealy endosperm to indicate a relationship with the Commelinaceae and Philydraceae. Hamann (in Melchior) suggested on embryological (starchy endosperm) and anatomical (unspecified) evidence that the Pontederiaceae should be separated from the Liliaceae but maintained as one of five suborders (including the Philydrineae) comprising the order Liliiflorae (Liliales), although he pointed out that in some characters the family is in agreement with the Commelinaceae (Commelinales) and Philydraceae.

Takhtajan stated that the Pontederiaceae probably originated from liliaceous stock, because of the presence of septal nectaries and similarities in vegetative anatomy and embryology (neither specified). Accordingly, he included a unifamilial Pontederiineae as one of six suborders (between the Haemodorineae and a unifamilial Philydrineae, the latter considered to be somewhat isolated but related to the Pontederiineae) in the Liliales, one of 14 orders (the Bromeliales and Commelinales among them) comprising the subclass Liliidae. Cronquist included the Pontederiaceae in his Liliales (subclass Liliidae), far removed from both the Bromeliaceae (Zingiberidae) and Commelinaceae (Commelinidae). Dahlgren, on the other hand, incorporated a unifamilial Pontederiales (between the Haemoderales and the Philydrales) as one of 12 orders with the Bromeliales in his Liliiflorae and placed the Commelinaceae in a separate superorder (Commeliniflorae). Dahlgren & Clifford envisioned a series of taxa, the members of which (e.g., Haemoderales, Philydrales, Pontederiales, Bromeliales, Commelinales) formed a gradual transition between the Liliiflorae and the Commeliniflorae and combined significant features of both. The Pontederiales were indicated to have substantially more attributes in common with "core" Liliiflorae (11 of 21) than with "core" Commeliniflorae (3 or 4 of 21) and a profile of features agreeing most closely with that of the Philydrales.

What little is known about the chemistry of the Pontederiaceae has been compiled and reviewed by Gibbs, and the following is based largely on that account. The plants are among only six monocot families (including none of those discussed here) for which the Mäule test (which is positive for all but weakly lignified tissues) is negative or doubtful. Calcium oxalate crystals, usually raphides, are present. Although cyanogenesis has been reported in *Monochoria*, Gibbs obtained negative results for *Eichhornia speciosa* Kunth, *Heteranthera dubia* (Jacq.) MacM., and *Pontederia cordata* L. He determined that mucilage was present in *Pontederia*, doubtfully so in *Heteranthera*, and absent in *Eichhornia*. Gibbs observed strong reactions between ferric ammonium citrate and the leaves of *E. speciosa* and *P. cordata*, indicating the likely presence of tannins or tanninlike substances; Cronquist (p. 1202) characterized the family as having "scattered tanniferous cells containing proanthocyanins." Saponins are reportedly absent or probably absent from *Eichhornia* and *Pontederia*. Lipids of *Eichhornia crassipes* (Mart.) Solms have been analyzed by Lakshminarayana and colleagues.

Various kinds of phenolic compounds are represented in the Pontederiaceae. Caffeic acid, cyanidin, and ferulic acid have been reported in *Eichhornia speciosa* and *Pontederia lanceolata* Nutt., while *p*-coumaric and synaptic acids are evidently known only from the latter (Bate-Smith). Leucoanthocyanins (which produce anthocyanidins when heated with mineral acids) were indicated for *P. cordata* by Gibbs and considered to be abundant in the family by Bate-Smith. The anthocyanins cyanidin, malvidin, delphinidin, and eichhornin have been reported in *E. crassipes* (see Krishnaveni *et al.*), as has been delphinidin in *P. lanceolata* (Bate-Smith). A number of other flavonoids, including the flavones apigenin and luteolin as well as the flavonols quercetin and isorhamnetin, were isolated from various species of *Heteranthera* by Horn (1985a).

Lowden compared the phenolic profiles of several genera of Pontederiaceae in his revision of *Pontederia* (see discussion of that genus).

Cheadle studied the vessel elements in a number of species (including five occurring in the Southeast) belonging to several genera of Pontederiaceae and found that they normally had long, obliquely oriented, scalariform perforation plates with many perforations and were mostly confined to the roots. Some, however, indicated a more advanced condition, because of either their structure (five or fewer perforations in nearly transverse plates) or their location (stems of *Eichhornia crassipes*, *Heteranthera limosa* (Sw.) Willd., and possibly *Pontederia cordata*). Cheadle concluded that while relatively unspecialized vessel elements are typical of aquatic angiosperms in general, the more advanced structure of some in the Pontederiaceae suggested that the family was primitively terrestrial. Nevertheless, he also allied the Pontederiaceae with the Philydraceae, even though the vessel elements in this group, which is terrestrial, are somewhat less specialized.

Anthers in the Pontederiaceae are tetrasporangiate (the normal condition among angiosperms); they are bisporangiate in the Philydraceae according to Bhandari, but are tetrasporangiate by Cronquist's account. The microspore mother cells undergo successive divisions to form either isobilateral or decussate tetrads (Davis), and the pollen grains are binucleate when shed (Brewbaker; see, however, Cronquist, who indicated that they are sometimes trinucleate).

The Pontederiaceae were not well known palynologically before Simpson's recent electron micrographic (both TEM and SEM) studies of the group (pers. comm.; 1986), which featured comparisons with the pollen of both the Haemodoraceae and the Philydraceae. Despite earlier reports to the contrary (Erdtman; Rao & Rao; Simpson, in press), pollen with two furrow-shaped apertures (orientation yet to be determined) appears to be the only type represented in the family. In part because this condition is unknown in either the Haemodoraceae or the Philydraceae (and presumably elsewhere), its derivation was considered to have been uniquely shared by members of the Pontederiaceae.

Internal exine structure is variable within the Pontederiaceae, according to Simpson (in press), but the variation does not correspond well to the tribes recognized here. For example, what was termed a "modified tectate-columellate" exine is shared by species of both the Heteranthereae (*Monochoria vaginalis* (Burman f.) Presl, *Scholleropsis lutea* H. Perr.) and the Pontederieae (*Pontederia cordata*), a "two-layered" exine characterizes members of both the Heteranthereae (*Zosterella dubia* (Jacq.) Small = *Heteranthera dubia*) and the Pontederieae (*Reussia rotundifolia* (L. f.) Castell. [here put in *Pontederia* subg. REUSSIA]), and a "one-layered" exine corresponding to the outer layer of the two-layered type was depicted for genera of the Eichhornieae (*Eichhornia crassipes*) and the Heteranthereae (*Hydrothrix Gardneri* Hooker f.). A condition described as intermediate between the modified tectate-columellate type and the two-layered type was reported for *Heteranthera reniformis* Ruiz & Pavón (see, however, Simpson, 1984).

On the basis of palynological evidence, Simpson also concluded that the Pontederiaceae are more closely related to the Haemodoraceae than to the

Philydraceae. The distinctive verrucate sculpturing reported for all the Pontederiaceae studied (except *Pontederia cordata*, which has psilate to scabrate pollen) is identical to that found in tribe Haemodoreae of the Haemodoraceae. In addition, two genera of Haemodoreae have a one-layered exine identical to that of *Eichhornia* and *Hydrothrix*, while four others in the Haemodoreae and all six genera of the Conostylideae have a two-layered exine very similar to that reported by Simpson for *Reussia* and *Zosterella*. The Philydraceae generally have reticulate grains and typical tectate-columellate internal exine structure.

The pontederiaceous ovule is anatropous, bitegmic (with both integuments forming the micropyle), and crassinucellar (Davis). The chalazal megaspore (see, however, Ono) of a linear tetrad develops into a Polygonum-type megagametophyte in which the synergids (at least in *Monochoria hastifolia* Presl) may have a filiform apparatus; the degree to which the three antipodals persist has been controversial (see Coker, R. W. Smith, W. R. Smith). Endosperm formation is, according to Davis, helobial, with free-nuclear divisions and subsequent wall formation normally taking place in both the micropylar and chalazal chambers (the chalazal chamber remains free-nuclear in *Monochoria*). Two haustorial arms are developed laterally in the micropylar chamber in *Monochoria* and presumably the remainder of the family as well (Davis). Embryogeny in the Pontederiaceae is of the Asterad type (see, for example, Souèges). The embryos, along with those of *Amomum* Roxb. (Zingiberaceae), are reportedly unique in their complete extension to both poles of the seed (Martin). According to information compiled by Davis, the most substantial embryological differences between the Pontederiaceae and the Philydraceae are that the former have an amoeboid (vs. glandular) tapetum and unhooked (vs. hooked) synergids.

Tristyly has been reported in the Pontederiaceae and three other flowering plant families (Lythraceae, Oxalidaceae, and Rubiaceae; see Vuilleumier). Species with this condition are characterized by individuals with one of three floral forms (morphs), each differing in the arrangement of anthers and stigmas. (For the condition in *Pontederia cordata*, see FIGURE 1, c-e.) Three levels (short, medium, and long) are occupied by two groups of anthers and the single stigma; thus, pollen is partitioned on a pollinator in such a way that its delivery to the stigma of another flower of the same morph is unlikely. For example, pollen from short and long stamens of mid-styled flowers normally would not be delivered to the stigmas of other mid-styled flowers. Transfers of pollen from anthers to stigmas of the same level are termed legitimate pollinations, while all intraform and some interform pollinations are illegitimate. Populations of tristylous Pontederiaceae (and perhaps other families) vary from isoplethy, a condition in which the three morphs are equally represented, to monomorphy, in which only a single floral form is present.

The mechanical barrier to pollinations leading to either self-fertilization or assortative (like genotype) crossing effected by the tristylous condition is normally accompanied by a physiological self-incompatibility system, as well as by a marked pollen trimorphism, and since the time of Darwin it has been thought to promote animal-mediated cross-pollination and subsequent out-

crossing. Under one argument tristylous and self-incompatibility are mutually reinforcing, while another holds that the former is secondarily reinforced by the latter, even though self-incompatibility would appear to be superfluous if the pollen partitioning effected by tristylous were as effective as it appears to be. It may be more reasonable to suppose that in groups with both conditions, self-incompatibility, which is relatively widespread in plants in general, evolved first and is secondarily reinforced by tristylous in the sense that pollen partitioning would minimize the wasteful placement of pollen on incompatible stigmas. The selective advantage of tristylous evidently does not involve reduction of interference on the stigma by illegitimate pollen or adjacent stamens, according to experiments on *Pontederia cordata* by Barrett & Glover. The pollen trimorphism accompanying tristylous in the Pontederiaceae, which involves differences in both pollen size and degree of self-incompatibility, appears to be physiological and/or developmental in nature and dependent on anther level (see discussions of *Eichhornia* and *Pontederia*).

Four species of *Pontederia* (*P. cordata*, *P. rotundifolia* L. f., *P. sagittata* Presl, *P. subovata* (Seub.) Lowden) and three of *Eichhornia* (*E. azurea* (Sw.) Kunth, *E. crassipes*, *E. paniculata* (Sprengel) Solms) are tristylous (Barrett, 1978a, 1979; Lowden; Richards & Barrett). The condition in *Pontederia* and *E. azurea* is accompanied by physiological self-incompatibility, strong pollen trimorphism, and populations in which all three floral morphs are usually represented, but it is characterized in *E. crassipes* and *E. paniculata* by a high degree of self-fertility, weakly developed pollen trimorphism, and populations that are frequently monomorphic. Self-fertilizing, semihomostylous (upper set of anthers adjacent to stigma) races of each of the tristylous species of *Eichhornia*, including *E. azurea*, have been reported (see also discussions of the genera).

Progeny tests have indicated that the determination of floral morph in *Eichhornia crassipes* is governed by two diallelic loci (Barrett, 1977). While the M locus determines whether styles are midlength (MM or Mm) or long (mm), the S locus controls whether they are short (SS or Ss) or nonshort (ss) and is epistatic to the M locus. Barrett, Price, & Shore have assumed that this pattern of inheritance characterizes all tristylous Pontederiaceae. (See further discussion under *Eichhornia* and *Pontederia*.)

The economic significance of the Pontederiaceae lies chiefly with *Eichhornia crassipes*, possibly the world's most serious aquatic weed; other members of the family also occur as weeds, especially in rice fields. A number of species have ornamental value, and many are used in one way or another by fish, waterfowl, aquatic mammals, and humans.

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COKER, W. C. The development of the seed in the Pontederiaceae. Bot. Gaz. **44**: 293–301. pl. 23. 1907. [Observations on *Eichhornia*, *Heteranthera*, *Pontederia*; illustrations of *H. limosa* and *P. cordata*; antipodals found to persist in *Heteranthera* and *Pontederia*, but see R. W. SMITH, W. R. SMITH.]

COOK, C. D. K., B. J. GUT, E. M. RIX, J. SCHNELLER, & M. SEITZ. Water plants of the world. viii + 561 pp. The Hague. 1974. [Pontederiaceae, 482–492; nine genera, line drawings.]

CORRELL, D. S., & H. B. CORRELL. Aquatic and wetland plants of southwestern United States. xvi + 1777 pp. Water Pollution Control Res. Ser., Environ. Protect. Agency. Washington, D. C. 1972. (Reissued in 2 vols. by Stanford Univ. Press. 1975.) [Pontederiaceae, 597–604; line drawings of *Eichhornia crassipes*, *Eurystemon mexicanum* (not known from the Southeast), *Heteranthera dubia*, *H. Liebmanii*, *H. limosa*, *H. reniformis*, *Pontederia cordata*.]

——— & M. C. JOHNSTON. Manual of the vascular plants of Texas. xv + 1881 pp. Renner, Texas. 1970. [Pontederiaceae, 366–368; *Eichhornia* (2 spp., both introduced), *Eurystemon* (monotypic), *Heteranthera* (4 spp.); forms (rosette vs. elongate stems) of *H. limosa* thought possibly to represent two species.]

CRONQUIST, A. An integrated system of classification of flowering plants. *Frontisp.* + xviii + 1262 pp. New York. 1981. [Pontederiaceae between Philydraceae and Haemodoraceae, one of 15 families in the Liliales; pollen indicated as sometimes trinucleate (other accounts mention only binucleate).]

CZAJA, A. T. Structure of starch grains and the classification of vascular plant families. *Taxon* **27**: 463–470. 1978. [Three groups of monocots based on starch grains and their carbohydrate substitutes: Pontederiaceae with Bromeliaceae, Commelinaceae, Philydraceae, Haemodoraceae, and others in “true” monocots (mature seeds with “highly compound starch grains,” vegetative organs with more than one type of starch grain and seldom with dissolved carbohydrates); Liliaceae and others in “derived” monocots (mature seeds seldom with starch grains, vegetative organs with starch and many other carbohydrates); the third group irrelevant here.]

DAHLGREN, R. M. T. A revised system of classification of the angiosperms. Bot. Jour. Linn. Soc. **80**: 91–124. 1980.

——— & H. T. CLIFFORD. The monocotyledons: a comparative study. xiv + 378 pp.

- London (and several other cities). 1982. [Liliifloreal attributes of Pontederiaceae include absence of silica bodies and presence of oxalate raphides, stem vessels (when present) with scalariform perforation plates, petaloid tepals, septal nectaries, sulcate pollen, binucleate pollen (see, however, CRONQUIST), axile placentation, several ovules per placenta, mostly capsular fruit, and linear embryos; commelinifloreal attributes include paracytic stomata, girdle type of endothelial thickenings, starchy (but not mealy) endosperm, and (possibly) absence of steroid saponins.]
- , S. ROSENDAL-JENSEN, & B. J. NIELSEN. A revised system of classification of the angiosperms with comments on correlation between chemical and other characters. Pp. 149–204 in D. A. YOUNG & D. S. SEIGLER, eds., *Phytochemistry and angiosperm phylogeny*. New York. 1981.
- DAUMANN, E. Das Blütennektarium bei den Pontederiaceen und die systematische Stellung dieser Familie. *Preslia* **37**: 407–412. 1965. [Septal nectaries present in *Eichhornia crassipes*, *E. paniculata*, *Pontederia cordata*, rudimentary in *Heteranthera reniformis*, lacking in *H. dubia* and *H. zosterifolia*; placement of family near Liliaceae (which lack septal nectaries) nevertheless favored; Pontederiaceae considered more primitive than Liliaceae, although descendant from a common ancestor.]
- DAVIS, G. L. Systematic embryology of the angiosperms. x + 528 pp. New York, London, and Sydney. 1966. [Pontederiaceae, 218, 219.]
- ECKENWALDER, J. E., & S. C. H. BARRETT. Phylogenetic systematics of Pontederiaceae. *Syst. Bot.* **11**: 373–391. 1986.* [South American origin for family, with several eastward dispersals; *Monochoria* and *Pontederia* monophyletic, *Eichhornia* and *Heteranthera* paraphyletic; heterostyly as a synapomorphy of only one lineage.]
- EICHLER, A. W. Blüthendiagramme. Erster Theil. 348 pp. Leipzig. 1875. [Pontederiaceae, 164–166.]
- ERDTMAN, G. Pollen morphology and plant taxonomy. Angiosperms. *Frontisp.* + xii + 539 pp. Uppsala. 1952. [Pontederiaceae, 335, 336; pollen of *Pontederia cordata* illustrated; pollen of family said to have two or three sulculi.]
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- FASSETT, N. C. A manual of aquatic plants. Revised ed., with Revision Appendix by E. C. OGDEN. ix + 405 pp. Madison and Milwaukee, Wisconsin, and London. 1957. [Pontederiaceae (*Heteranthera*, *Pontederia*), 171–173; illustrations, including those of several forms of *P. cordata*.]
- GIBBS, R. D. Chemotaxonomy of flowering plants. Vols. 1–4. 2372 pp. Montreal and London. 1974. [Vol. 4 includes bibliography, index, and addendum; numerous references to Pontederiaceae.]
- GODFREY, R. K., & J. W. WOOTEN. Aquatic and wetland plants of southeastern United States. Monocotyledons. xii + 712 pp. Athens, Georgia. 1979. [Pontederiaceae, 534–541; *Eichhornia crassipes*, *Heteranthera dubia*, *H. reniformis*, *Pontederia cordata* (vars. *cordata* and *lancifolia* said to be often indistinguishable; variation great in southern Georgia and throughout Florida, where varieties overlap); all taxa illustrated.]
- HEGNAUER, R. Chemotaxonomie der Pflanzen. Band 2. Monocotyledoneae. 540 pp. Basel and Stuttgart. 1963. [Pontederiaceae, 419–421; *Eichhornia crassipes* with alkaloids, hydrocyanic acids, and possibly triterpenes by one account, lacking alkaloids, saponins, and tannins by another; neither alkaloids nor saponins detected in *Pontederia cordata*.]
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Heteranthera dubia, *H. reniformis*, *Pontederia cordata*; illustrations, distribution maps.]

- HESLOP-HARRISON, Y., & K. R. SHIVANNA. The receptive surface of the angiosperm stigma. *Ann. Bot.* II. **41**: 1233–1258. 1977. [*Eichhornia*, *Pontederia* said to have unicellular papillae on dry stigmas.]
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- HORN, C. N. Anatomical adaptations to the aquatic environment in the Pontederiaceae, its taxonomic usefulness. (Abstr.) *ASB Bull.* **31**: 62. 1984a. [*Eichhornia*, *Heteranthera*, *Hydrothrix*, *Pontederia*, and *Zosterella* considered; all seedlings initially produce linear, nonpetiolate leaves; anatomical variation adaptive, of little taxonomic value.]
- . A systematic revision of the genus *Heteranthera* (*sensu lato*, Pontederiaceae). xiv + 260 pp. Unpubl. Ph.D. dissertation, Univ. Alabama, University. 1985a. (*Diss. Abstracts B.* **46**(7): 2174. 1986.)
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- HUNTER, C. G. *Wildflowers of Arkansas*. viii + 296 pp. Ozark Society Foundation, Little Rock, Arkansas. 1984. [Pontederiaceae, 32, 33; *Heteranthera limosa* and *Pontederia cordata* illustrated in color.]
- HUTCHINSON, J. *The families of flowering plants*. ed. 3. xx + 968 pp. Oxford. 1973. [Pontederiaceae, 761–764.]
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- LAKSHMINARAYANA, G., K. SUNDAR RAO, A. J. PANTULU, & G. THYAGARAJAN. Composition of lipids in roots, stalks, leaves and flowers of *Eichhornia crassipes* (Mart.) Solms. *Aquatic Bot.* **20**: 219–227. 1984.
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- MASON, H. L. *A flora of the marshes of California*. ix + 878 pp. + errata. Berkeley and Los Angeles. 1969. [Pontederiaceae, 343–347; *Eichhornia crassipes* naturalized and locally abundant, mostly in San Joaquin and Sacramento valleys; *Heteranthera dubia*

- known from few localities, perianth tubes much shorter than those elsewhere in U. S.; *Monochoria vaginalis* locally established in experimental rice plots, native to India and southeastern Asia); line drawings.]
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- OGDEN, E. C. Anatomical patterns of some aquatic vascular plants of New York. New York State Mus. Sci. Serv. Bull. 424. v + 133 pp. 1974. [Transsectional illustrations of *Heteranthera dubia* (pl. 38; stem, peduncle), *Pontederia cordata* (pl. 39; stem).]
- OLIVE, E. W. Contributions to the histology of the Pontederiaceae. Bot. Gaz. 19: 178–184. pl. 17. 1894. [Long crystals of calcium oxalate in *Eichhornia crassipes* and *Pontederia cordata*; those in *Heteranthera limosa* evidently much shorter.]
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- RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Chapel Hill, North Carolina. 1968. [Pontederiaceae, 272, 273; *Eichhornia crassipes*, *Pontederia cordata* (including *P. lanceolata* Nutt.), *Heteranthera dubia*, *H. reniformis* (restricted to northeastern North Carolina).]
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- . Zur Systematik und Geographie der Pontederiaceen. Studien zu einer Monographie der Familie. Bot. Jahrb. **61**(Beibl. 139): 28–50. 1927. [Protologues and justifications for tribes and sections later employed in *Die natürlichen Pflanzenfamilien*.]
- . Pontederiaceae. Nat. Pflanzenfam. ed. 2. **15a**: 181–188. 1930.
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- . Pollen ultrastructure of the Pontederiaceae: evidence for exine homology with the Haemodoraceae. Grana (in press). [Exine sculpturing and architecture said to indicate close relationship between the two families (pers. comm.).]
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- . Manual of the southeastern flora. xxii + 1554 pp. Chapel Hill, North Carolina. 1933. [Pontederiaceae, 265–268; *Eichhornia crassipes* (*Piaropus crassipes*) thought to be native in interior peninsular Florida.]
- SMITH, R. W. Endosperm of Pontederiaceae. Bot. Gaz. **45**: 338, 339. pls. 1–4. 1908. [Illustrations of megagametophyte development in *Pontederia*; cells deteriorate but nuclei of antipodals persist in *Eichhornia* and *Pontederia*; see, however, COKER, W. R. SMITH.]
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- VOSS, E. G. Michigan flora. Part I. Gymnosperms and monocots. xviii + 488 pp. 8 pls. Bloomfield Hills, Michigan. 1972. [Pontederiaceae, 378, 379.]
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- WIT, H. C. D. DE. Aquarium plants. (English translation by J. A. SCHUURMAN.) *Frontisp.* + 255 pp. London. 1964. [*Heteranthera*, 207, 208; *H. dubia* thought to occur most often in alkaline water; *H. reniformis* thought to tolerate brackish water.]
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KEY TO THE GENERA OF PONTEDERIACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: Rooted or floating herbs, submersed, emersed, or sometimes on wet ground; stems sympodial, either stout and sometimes connected by stolons or elongate; leaves simple, alternate, sessile and ligulate or petiolate, venation parallel, a distinct midvein absent, bases sheathing; inflorescences terminal (often appearing axillary), spicate, racemose, paniculate, or single flowered, sessile or pedunculate, each subtended and enclosed to various extents by a sheathing bract that is sometimes surmounted by a reduced petiole and/or blade, each flowering stem with a single leaf sometimes differing from the others; flowers perfect (some species tristylous); perianth of 6 petaloid tepals in 2 series, the lobes imbricate, fused to various degrees basally, actinomorphic to zygomorphic (then with 2 lips of 3 lobes each); stamens usually 6 or 3 (and then sometimes with 3 staminodes), the filaments adnate to perianth tube, inserted at various levels (often in the same flower), the anthers usually with introrse, longitudinal dehiscence; carpels 3, united; style single; ovary superior with 1 or 3 fertile locules; nectaries septal or absent;

ovules solitary (in unilocular ovaries) or numerous in each locule, anatropous, bitegmic; fruit a 1-seeded utricle or a many-seeded capsule; seeds small, those in capsules with longitudinal ridges.

- A. Inflorescences usually several- to many-flowered; perianths zygomorphic; stamens 6 (at least in chasmogamous flowers), long axes of anthers and filaments not parallel; nectaries septal.
- B. Ovaries with 3 fertile, many-ovulate locules; fruit a capsule; plants usually floating. 1. *Eichhornia*.
- B. Ovaries with 1 fertile, 1-ovulate locule (and 2 aborted locules); fruit a utricle; plants rooted in substrate. 3. *Pontederia*.
- A. Inflorescences usually 1- to few-flowered; perianths actinomorphic or subactinomorphic; stamens 3 (at least in chasmogamous flowers), long axes of anthers and filaments parallel; nectaries absent. 2. *Heteranthera*.

Tribe EICHHORNIEAE Schwartz, Bot. Jahrb. **61**(Beibl. 139): 32. 1927.

1. **Eichhornia** Kunth, *Eichhornia*, Genus Novum [Diss.]. 1842; Enumeratio Pl. **4**: 129. 1843, nom. cons.

Perennial [or annual], submersed, emersed, or floating herbs. Stems stout, more or less vertical, often connected by stolons. Adult leaves exstipulate, either sessile, linear, and thin (if submersed), or petiolate, with the petioles longer than the blades and usually more or less inflated, the blades broadly elliptic to orbicular. Inflorescence a spike or panicle [or single flowered], pedunculate, the subtending bract of each with a highly reduced petiole and blade, the single leaf on each flowering stem with a large, sheathing base, little or no petiole, and a reduced blade. Flowers perfect, some species tristylous; perianth mostly funnelform, zygomorphic, with 2 lips of 3 lobes each. Stamens 6, unequal in length; filaments curved; anthers oblong, auriculate and somewhat movable on the filaments, much shorter than the filaments, the adaxial 3 either included deep within the perianth tube or near its summit, lower than the abaxial 3, which are either near the summit of the perianth tube or exserted. Ovary with 3 locules, each with numerous ovules on an axile placenta; stigma (depending on style length) included deep within the perianth tube, or near its summit, or exserted. Fruit a many-seeded, membranaceous capsule with loculicidal dehiscence; seeds longitudinally ribbed. (*Eichornia* A. Rich., 1850, orthographic variant; *Piaropus* Raf., 1837, nom. rejic.) TYPE SPECIES: *E. azurea* (Sw.) Kunth (*Pontederia azurea* Sw.), typ. cons. (Named for Johann Albrecht Friedrich Eichhorn, of Berlin, 1779–1856.)—WATER HYACINTH.

A genus of about seven species native to the American tropics and perhaps subtropics, including one, *Eichhornia natans* Solms, that appears to be closely related to (if not conspecific with) plants that may occur naturally in tropical Africa and Madagascar, and another, *E. crassipes* (Mart.) Solms, that through introductions has spread throughout the tropics and to adjacent warm-temperate areas. *Eichhornia* can be distinguished from other genera of Pontederiaceae by a combination of floral characters including a mostly funnelform perianth, six stamens, and an ovary with three fertile, many-ovulate locules.

Schwartz (1927, 1930) placed *Eichhornia* in the monogeneric tribe Eichhornieae Schwartz and proposed two sections in the genus that were neither ad-

equately defined by him nor widely accepted by later workers (e.g., Alexander, Castellanos, Schulz), although they may have some utility. Section PROTO-EICHHORNIA Schwartz (paniculate inflorescences, plants rooted in the ground) included *E. paniculata* (Sprengel) Solms and *E. paradoxa* (Mart.) Solms, while sect. *Eueichhornia* Schwartz (= EICHHORNIA) (spicate inflorescences, plants free floating) included *E. azurea* (Sw.) Kunth, *E. natans*, and *E. crassipes*. Additional names, and perhaps species, exist, and the genus is in need of taxonomic attention on a worldwide basis.

Two species of *Eichhornia* have been reported from the southeastern United States, each an introduction, apparently from Brazil. *Eichhornia paniculata* differs from *E. crassipes*, $2n = 32$, in the characters by which the two sections are distinguished and in its complete lack of inflated petioles. It was at least at one time naturalized in peninsular Florida from plants in cultivation (Alexander; Muenscher, 1944), but I have seen no specimens from the area and the species is not included in recent floristic accounts (e.g., Godfrey & Wooten, Long & Lakela, and Ward). *Eichhornia azurea*, $2n = 32$, also lacking inflated petioles, is an introduction in southern Texas (Correll & Correll).

Perianths in *Eichhornia*, including those of our plants, are various intensities of blue, violet-blue, or lilac, with those of *E. crassipes* often pale and rarely even white; those of *E. paniculata* are often darker in the lower three lobes. The upper-middle perianth lobe in *E. crassipes* usually bears a deep violet-blue area with a yellow spot inside, while that of *E. paniculata* has an unbordered, bilobed yellow spot (Alexander).

Eichhornia crassipes, the water hyacinth, is generally considered to be the world's most serious aquatic weed. An enormous amount of research has been conducted in an effort to understand many aspects of its biology, with the ultimate but perhaps unattainable goal of eradicating it from areas and habitats in which it is not native. The literature on this species, which has been reviewed by Sculthorpe and more recently by Pieterse, is correspondingly immense. The *Hyacinth Control Journal* (now the *Journal of Aquatic Plant Management*), the existence of which underscores the significance and extent of the problem, contains only a portion of what has been published.

Problems caused by the water hyacinth, although multifarious, are all more or less direct results of the tremendous, rapidly accumulated biomass generated by the plants. Floating mats are frequently large enough to obstruct navigation completely, to impede drainage to the point of flooding, to contribute in various ways to eutrophication, and to cause wastage of impounded water by displacement and transpiration. It was conservatively estimated that in Louisiana damage and losses attributable to the foregoing probably exceeded five million dollars per year in the 1940's (Penfound & Earle). The water hyacinth has been reported to have detrimental effects on rice paddies (Sculthorpe) and to provide excellent conditions for mosquitoes and other disease-carrying organisms (Vietmeyer). The floating mats are thought to accelerate greatly and perhaps alter fresh-water succession (see Sculthorpe) and to prevent the occupancy of lakes, ponds, and streams by various kinds of waterfowl (Vietmeyer).

Methods of controlling the water hyacinth have been both numerous and

varied. Removal of the plants by hand has been effective in small waterways and rice fields, but this may be hazardous if disease-carrying organisms are present and is impractical if the mats have attained even relatively small sizes. Various devices (including lasers) have been constructed either to cut temporary paths through the mats or to destroy them completely, but the costs involved have been high. Numerous chemicals, most commonly 2,4-dichlorophenoxyacetic acid (2,4-D), have been employed, but effects on the environment have usually been detrimental. Drainage of infested areas has been effective in killing the plants, but this may ultimately prove to be unwise because it favors seed production, which could enhance the adaptability of the species. Many control methods result in the accumulation of dead and decaying plant material that must be removed in order to prevent eutrophication.

Attempts at biological control have included the use of fungi, snails, mites, insects, fish, and manatees. Significant control by the host-specific weevil *Neochetina eichhorniae* Warner has been reported in Louisiana (Goyer & Stark) and in Florida (Center & Durden); *N. bruchi* Hustache and the pyralid moth *Sameodes albiguttalis* (Warren) have also been released in Florida (Center & Durden). Center & Durden (p. 28) note that "recent successes with biological control of water hyacinth. . . have now been reported worldwide."

Accounts regarding the first appearance of *Eichhornia crassipes* in the United States are somewhat varied (see Penfound & Earle). Despite some evidence that it was cultivated shortly after the Civil War, it was, according to some, first shown at an exposition in New Orleans in 1884. The plant attracted a great deal of attention as a beautiful, easily grown ornamental. Because of its popularity and vigorous growth, its escape from cultivation and subsequent naturalization were probably inevitable. In Louisiana, and elsewhere in the world, its introduction to nature was commonly effected by exasperated gardeners who, in attempting to rid cultivated pools and ponds of this initially desirable but soon troublesome aquatic, threw living material into local waterways in the hope that it would be carried away. Unfortunately, the plants thrived out of cultivation in areas where natural enemies were lacking. The species was reported from Florida in 1890, was known from each of the coastal states in the Southeast (its maximum and present range in our area) by the early 1900's, and was first recorded in California in 1904 (Bock, 1968). Nevertheless, in North America it appears to have been and continues to be a serious problem only in Louisiana, Mississippi, and Florida (Sculthorpe).

The water hyacinth, a native of the South American tropics, has been introduced and is now naturalized throughout most tropical and subtropical areas of the world, with an adventive range extending into such warm-temperate areas as the southeastern United States, California, Japan, southeastern China, northern Africa, Portugal, Uruguay, and South Africa (for distribution map, see Barrett, 1977, or Sculthorpe, p. 462). Although it is called the "Florida devil" in South Africa (Vietmeyer), and although its introduction throughout the Old World seems to postdate its first occurrences in North America, it is unclear whether the species spread secondarily from that continent or was introduced outside of the Western Hemisphere directly by plants obtained from

South America. It seems likely that both contributed (see also discussion of style morph distribution, below). It was introduced into Malaysia in 1894 (Backer).

The plants can rapidly cover stagnant or slow-moving bodies of fresh water because of their remarkable capacity for vegetative growth and reproduction. A single plant reportedly developed in one season into a patch of about 600 m² through the production of a radiating system of stolons and associated rosettes (Aston; see also Batanouny & El-Fiky). The foliage is killed by frost or generally cold conditions, but the stems may survive and resume growth when temperatures rise. Unconfirmed reports indicate that although the plants are sensitive to salt water, stems protected by sheathing leaf bases may survive exposure long enough for dispersal along sea coasts (Vietmeyer); stems so protected may also withstand periods out of water. Seeds remain viable for up to 15 years and may aid in dispersal of the plants, as well as in their reestablishment following extermination of the parental plants.

Although it has been difficult to assess the relative importance of reproduction by seeds in the spread of *Eichhornia crassipes*, there is now little doubt that it has been very much underestimated in the past. While Hitchcock and colleagues reported very few seedlings in Louisiana despite extensive seed production, tremendous numbers of young plants were discovered along the banks of the White Nile in November, 1963, less than six years after the species was first seen in the region (Pettet). Ironically, the massive establishment is thought to have resulted from attempts to eradicate the species with 2,4-D. The seedlings were most abundant on the decomposed material left by the killed mats of *E. crassipes* and were absent from adjacent banks of natural, sandy soil. The free-floating habit of *E. crassipes* often limits sexual reproduction, particularly in the adventive range of the species, by enabling the plants to reach and then occupy habitats that never become favorable for germination and seedling establishment. In habitats with seasonally fluctuating water levels, which are more commonly occupied in the native range of the species, sexual reproduction may be very important, since seeds germinate and seedlings become established in warm, shallow water during periods of extensive desiccative damage to vegetative parts.

Barrett (1980a, 1980b) determined that clones of *Eichhornia crassipes* from Louisiana, Florida, California, Mexico, South America, Africa, and India all retained the potential for sexual reproduction and that observations to the contrary were due to environmental and not genetic factors. Sexual reproduction in nature is evidently limited by inadequate pollination and unsuitable conditions for seed germination and seedling growth and not by the inbreeding depression, self-incompatibility, and accumulation of deleterious mutations often characteristic of largely vegetative species.

The free-floating habit and vigorous asexual reproduction of *Eichhornia crassipes* have been held responsible in one way or another for the reported disruption of tristylly in the species. These features have often resulted in populations that are either monomorphic (particularly in the adventive range of the species) or dominated by a single floral form. In either case selection has presumably favored the development of self-compatibility, high levels of which

have been detected in many populations (Barrett, 1977; François; Mulcahy). Barrett (1979) studied a marshland population in Costa Rica consisting of both mid- and long-styled forms and determined that within each, seed production following illegitimate pollinations was only slightly less than that associated with legitimate pollen deposition, indicating both self-compatibility and weak and/or residual self-incompatibility. The results of progeny tests involving seeds obtained from these plants revealed low levels of disassortative (unlike genotype) crossing for each floral form. While this pattern of crossing is at least in part due to pollinator behavior (foraging bees tended to visit most of the flowers of an inflorescence before departing), it also indicates high levels of self-compatibility.

The habit and growth characteristics mentioned above have further contributed to the disruption of tristily in *Eichhornia crassipes* by allowing the plants to occupy extensive areas, particularly within the adventive range of the species where pollinators are supposedly ill adapted and/or limiting (Barrett, 1977). Flowers within the native range of *E. crassipes* are usually visited by insects large enough to partition the different pollen types effectively and thereby to cross-pollinate the three floral forms (e.g., *Ancyloscelis gigas*, a species of long-tongued bee, is the major pollinator in the lower Amazon). Flowers in the adventive range, on the other hand, have apparently been attracting smaller pollinators, so there has been selective pressure to bring the anthers and stigmas closer together. Such floral modifications would also be favored if pollinating vectors were numerically limiting because they would increase the chances of self-pollination. Barrett (1979) reported that four percent of the mid-styled flowers sampled from a Costa Rican population considered to be outside the native range of the species were semihomostylous (upper set of anthers adjacent to stigma; also reported by François) and that this condition was accompanied by increases in pollen deposition. The development of semihomostyly and related phenomena is probably responsible at least in part for the weakened pollen trimorphism observed as another aspect of the breakdown of tristily in *E. crassipes* in that size and number of pollen grains are dependent on anther level (Barrett, 1979).

Semihomostyly in *Eichhornia crassipes* is generally thought to have been derived from tristily because its occurrence is restricted and because it evidently has not been detected in the native range of the species. Reports of the condition throughout *E. heterosperma* E. J. Alex., *E. natans*, and *E. diversifolia* (Vahl) Urban (see Barrett, 1979), as well as in races of *E. azurea* (Barrett, 1978a), prompted Barrett (1979) to conclude that it developed a number of times within the genus. Its relative infrequency in *E. crassipes* appears to be the result of limited sexual reproduction and consequently slow evolutionary rates within the species (Barrett, 1979).

Investigations into the distribution of style-morphs among New World populations of *Eichhornia crassipes* have suggested that the species is native to the Amazon basin and perhaps to parts of the Paraguay and Paraná river systems, as well, instead of to the tropics and subtropics of the New World in general, as has been widely thought (see primarily Barrett & Forno). Trimorphic populations, which if of limited occurrence would be expected primarily in areas

of ancient occupancy (assuming that the species is indeed primitively tristylous), have been reported only from the Amazon basin in Brazil (where the species is thought to have originated) and from lagoons near the confluence of the Paraguay and Paraná rivers in Argentina (to which it is thought to have spread by natural means). Populations in Paraguay, Uruguay, Guyana, Venezuela, and Colombia, as well as throughout the Caribbean, Central America, and warm-temperate North America, evidently lack the short-styled morph and are therefore considered to have resulted from introductions. (The lack of specialized pollinators in Central America also implies that the species is introduced there.)

Distribution data on style-morphs may provide insights into the spread of *Eichhornia crassipes* when considered in conjunction with the genetic basis of tristily in the species. Since the short-styled morph (S__M__ or S__mm) cannot be segregated from crossings involving the mid- (ssM__) and/or long-styled (ssmm) morphs, its presence in the adventive range of the species would have required separate introduction(s). The fact that it is evidently absent from these areas suggests that the spread of the species throughout the world has involved only a very few and perhaps even a single introduction, unless the short-styled morph for some reason either was not selected by man from nature or is ill equipped to become introduced and established outside its native range. Otherwise, one would expect at least some introductions to have involved the short-styled morph. The predominance of the mid-styled form in the adventive range and of the short-styled morph in the native range (Barrett & Forno) would then be explained by simple genetics. That seed production of the short-styled morph in the Lower Amazon was found to be 44–75 percent higher than that of the other two style-morphs (Barrett, 1977, 1980a) is not only consistent with the foregoing but may imply that it de-emphasizes vegetative reproduction and is therefore less well adapted to establishment outside its native range.

Considerable effort has been expended to find uses for *Eichhornia crassipes* on the assumption that exploitation would constitute the most economically sound form of control (see primarily Pieterse). Plants have been investigated as animal fodder (silage, hay, pelletized feed), but their high water content has made harvesting, storage, and processing difficult. The costs of using the water hyacinth as fertilizer and mulch have also been prohibitive. The plants have been utilized with some success as sources of plant hormones and other chemicals and have been fermented to produce methane. Because the roots of *E. crassipes* are effective in absorbing nitrates, phosphates, and potassium, the species has been used to purify water that has been polluted by fertilizers. Fishermen in the Philippines and in Bangladesh maintain circular mats that provide shade and shelter and therefore attract fish, and farmers in Bangladesh and Burma transform mats into floating gardens by the application of fertile bottom muck. Neither the water hyacinth if grown for a crop nor the plants grown on the floating gardens require manufactured fertilizer, irrigation, or land. Leaves of water hyacinth are used in Thailand to wrap cigars and are utilized by the Chinese in wicker and basket work.

REFERENCES:

Under family references see ALEXANDER; ASTON; BACKER; BARRETT (1978a, 1979); CASTELLANOS; CORRELL & CORRELL; GODFREY & WOOTEN; LONG & LAKELA; MUENSCHER

(1944); SCHULZ; SCHWARTZ (1927, 1930); SCULTHORPE; and WARD. See also the *Journal of Aquatic Plant Management* (formerly the *Hyacinth Control Journal*) and *Aquatic Botany*.

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Tribe HETERANTHEREAE Schwartz, Bot. Jahrb. **61**(Beibl. 139): 35. 1927.

2. **Heteranthera** Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 9. 1794, nom. cons.

Perennial or annual, submersed, emersed, or floating herbs. Stems stout and more or less vertical to elongate and more or less horizontal. Adult leaves stipulate or exstipulate, either sessile, linear (strap shaped) and thin, or petiolate, with the petioles longer than the blades and not inflated, the blades reniform, cordate, or lanceolate. Inflorescence a spike or single flowered, sessile or pedunculate, the subtending bract lacking a petiole and blade, the single leaf on each flowering-stem identical to all other leaves. Flowers perfect; perianth salverform, with 6 lobes, actinomorphic or subactinomorphic (1 lobe different in shape and/or spaces between lobes unequal). Stamens 3 (sometimes 1 in cleistogamous flowers), equal in length or the lateral 2 shorter, inserted on adjacent adaxial tepals; filaments straight or curved; anthers oblong or ovate, sometimes auriculate and somewhat movable on the filaments, sometimes nearly equal in length to the filaments, exserted, in subgen. *Zosterella* becoming circinately coiled after anthesis. Ovary with 1 locule, the ovules numerous in 2 or more rows on each of 3 more or less completely intrusive placentae; stigma usually exserted. Fruit a many-seeded membranaceous capsule with loculicidal dehiscence; seeds longitudinally ribbed. (*Schollera* Schreber, 1791, not Roth, 1788; *Heterandra* Beauv., 1799; *Leptanthus* Michx., 1803, nom. superfl. [includes type of *Heterandra* Beauv.]; *Zosterella* Small, 1913; *Eurystemon* E. J. Alex., 1937.) TYPE SPECIES: *H. reniformis* Ruiz & Pavón, Fl. Peruv. Chil. **1**: 43. 1798. (Name from Greek *heteros*, different, and *antheros*, anther, in reference to the unequal anthers of most species, including the type.)—MUD-PLANTAIN, WATER STAR-GRASS, BUFFALO-GRASS.

A small genus of about 12 species native to tropical and temperate regions of the New World and Africa. *Heteranthera* is distinguished from other Pontederiaceae by a suite of floral characters, including salverform perianths with six equal or nearly equal lobes, one- or imperfectly three-loculate ovaries with numerous ovules, and three stamens.

Infrageneric classifications of *Heteranthera* have been varied. Persoon (1805) evidently was the first to subdivide the genus (as *Leptanthus* Michx.), establishing two subgenera (see Brizicky) based on androecial morphology: *Heteranthera* (including the types of both *Heteranthera* Ruiz & Pavón and *Heterandra* Beauv.), with dimorphic stamens (“Filam. longitudine inaequalia, antherae bifformes”); and *Leptanthus*, with stamens of only one form (“Antherae uni-

formes lineares, filamenta aequalia"). Solms-Laubach later (1883a) established two sections: *Leptanthus* Solms (including the type of *Heteranthera*), with petiolate leaves; and *Schollera* Solms, with strap-shaped (ligulate) leaves. Schwartz (1927) recognized three sections on entirely different grounds. Section *Protoheteranthera* (= sect. HETERANTHERA) was characterized by three- to many-flowered inflorescences with no cleistogamous flowers; sect. *Heterantheropsis*, by one- or two-flowered inflorescences with no cleistogamous flowers; and sect. *Euheteranthera*, by many-flowered inflorescences with one or more cleistogamous flowers.

Small (in Small & Carter) segregated the monotypic genus *Zosterella* from *Heteranthera* on the basis of monomorphic (vs. dimorphic) stamens and linear (vs. broad) leaf blades. Although such a treatment generally agrees with that of Persoon, neither has been widely accepted. Recent studies by Horn (1985a), however, suggest that division of *Heteranthera* along these lines may be most tenable. Neither leaf morphology, on which the classification of Solms-Laubach was based, nor the presence or absence of cleistogamous flowers, by which Schwartz's sections were partially delimited, has proven to be taxonomically significant. Horn (1984a) reported that all species in the group initially produce strap-shaped (linear) leaves and that the mature leaf form is habitat dependent. Horn (1985a) also determined that all species produce cleistogamous flowers, usually in response to development under water, and that such structures are for the most part morphologically identical to chasmogamous flowers (see also Thieret). Underwater development commonly results in reduced numbers of flowers per inflorescence as well, unless the species is one that normally produces only one- or two-flowered inflorescences.

Horn (1985a) recently completed a revision of *Heteranthera* sensu lato that employed a number of biosystematic methods (e.g., flavonoid chemistry, cytology, pollen and seed morphology, vegetative anatomy, developmental biology), as well as numerical (cluster and principal component) and cladistic analyses of populations and species, respectively. Although a fairly convincing case for the existence of two groups was presented, I do not agree that the data support their recognition at the generic level (*viz.*, *Heteranthera* and *Zosterella*). Horn's decision to do so may have resulted from a failure to incorporate out-group comparisons in the analyses: the characters by which *Heteranthera* and *Zosterella* were reported to differ (e.g., internode length on flowering stem, length of time flowers stay open, perianth pubescence, androecial morphology [monomorphic or dimorphic stamens], filament inflation, anther shape and coiling, seed size) seem much less significant than those by which other genera in the Pontederiaceae differ (e.g., fusion of perianth parts, number of stamens, attachment and dehiscence of anthers, number of locules per ovary and of ovules per locule, and fruit type). In addition, the stamens of *H. limosa* (Sw.) Willd. and *H. peduncularis* Benth are only slightly dimorphic (indeed, Persoon included *Leptanthus ovalis* Michx. [= *H. limosa*] in subg. *Leptanthus*; Horn, however, has correctly placed it with the other species having dimorphic stamens), further lessening the distinction between the two groups. I am, therefore, recognizing as subgenera the two groups treated as genera by Small and

Horn.³ The species concepts of Horn appear to be sound, and much of the following is based on his revision. (Unless otherwise indicated, material attributed to Horn is taken from his dissertation.)

Subgenus *HETERANTHERA* (annuals with dimorphic stamens and noncoiling anthers) comprises the eleven species placed by Horn in *Heteranthera* sensu stricto; all but one (*H. callifolia* Reichenb. ex Kunth, of sub-Saharan Africa) are native to the New World. Two groups were identified in subg. *HETERANTHERA* by Horn's cladistic analysis, although they were not given names (see, however, Horn, 1986b). One group of species, all $2n = 14$, is represented in the Southeast by *H. limosa* and probably by *H. rotundifolia* (Kunth) Griseb. The other group, in which $x = 8$, has among its members *H. multiflora* (Griseb.) Horn, $2n = 32$, and *H. reniformis* Ruiz & Pavón, $2n = 48$, both found in our area. All species of the subgenus in our area produce petiolate leaves.

Heteranthera limosa and *H. rotundifolia*, each with single-flowered inflorescences, are identical in flavonoid chemistry, chromosome number, and pollen and seed morphology. Plants of *H. limosa* commonly form rosettes and have ovate to elliptic leaf blades, actinomorphic perianths, and nearly monomorphic stamens, while those of *H. rotundifolia* do not form rosettes and have at least some round leaf blades, subactinomorphic perianths (one lobe cordate at the base), and clearly dimorphic stamens (the lateral filaments curved). Plants of *H. limosa* usually occur in shallow water, commonly at the edges of ponds and in roadside ditches, and are submersed as seedlings. Rosette-forming individuals and others with elongate, horizontal stems occur in the Southeast and may represent two biologically meaningful taxa, according to Correll & Correll, although Horn considered the latter condition to be induced by growth in water 10 cm or more deep. The distribution of *H. limosa* extends from California and the central United States (including Tennessee, Mississippi, Arkansas, and Louisiana) to central South America. Plants of *H. rotundifolia* grow in small bodies of water or on mudflats. With the exception that the species has not been reported either from California or from our area, it has a distribution almost identical to that of *H. limosa*. Although Steyermark did not report *H. rotundifolia* from Missouri (he apparently did not consider it to be distinct from *H. limosa*), Horn indicated that it occurs throughout the state and along the Missouri side of the Arkansas border.

³Although *Schollera* Schreber is a later homonym and is therefore illegitimate at the generic level, it could be used as a new name for the subgenus with monomorphic stamens recognized here. However, *Zosterella* Small is also available, and since it is the more familiar name for these plants, it is appropriate to make the following new combination at the level of subgenus.

***Heteranthera* subg. *Zosterella* (J. K. Small) Rosatti, comb. et stat. nov.**

Zosterella J. K. Small in J. K. Small & J. J. Carter, Fl. Lancaster County [Pennsylvania], 68. 1913.

TYPE SPECIES: *Z. dubia* (Jacq.) J. K. Small (*Commelina dubia* Jacq.).

Leptanthus Michaux (1803) is a superfluous name, since Michaux cited *Heterandra* Palisot de Beauvois (Trans. Am. Philos. Soc. 4: 175. 1799) (as "*Heteranthera*"), for which the type species is *Heterandra reniformis* Beauv., 1799, not *Heteranthera reniformis* Ruiz & Pavón, 1798, although both names apply taxonomically to the same species.

Heteranthera multiflora and *H. reniformis* both have spicate inflorescences, and they are difficult to distinguish vegetatively. However, in *H. multiflora* the flowers are purple, and the inflorescence is more than twice as long as the subtending bract, while in *H. reniformis* the perianths are white and the spike is usually about as long as the bract. In the United States *H. reniformis* occurs from Connecticut and southern New York southward to southeastern Virginia, western North Carolina, northern Georgia, and western Florida, and westward to Louisiana, southern and western Missouri, and southern Illinois, with disjunct localities along the Rio Grande in Texas. It is also found in Mexico and Central America, Cuba, Hispaniola, and Jamaica. In South America it is known from Venezuela and Colombia, southward to northern Argentina, Paraguay, and southern and eastern Brazil. *Heteranthera multiflora* has a similar but more disrupted distribution. In the United States it is known from New Jersey south to northeastern North Carolina; from southwestern Illinois, Missouri, southeastern Nebraska, Kansas, Oklahoma, Arkansas, and southwesternmost Tennessee; and from outlying stations in Mississippi and southernmost Texas. Disjunct localities have been found in northern Venezuela, northern Argentina, Paraguay, and southern and eastern Brazil. Although plants of both species can either float or become rooted in shallow water or moist ground, those of *H. multiflora* reportedly are able to occupy deeper water than those of *H. reniformis* because of their superior ability to produce elongate stems. *Heteranthera peduncularis*, primarily of high elevations in Mexico but also reported from southeastern Arizona and Guatemala, is very similar to *H. multiflora* and *H. reniformis* but can evidently be distinguished from them by its glabrous or glabrate (vs. pubescent) lateral staminal filaments.

Subgenus ZOSTERELLA (perennials with monomorphic stamens and coiling anthers) comprises one, or perhaps two, species, both present in the Southeast. The leaves are linear in both and resemble those of *Potamogeton* species, except that they lack a distinct midrib. *Heteranthera Liebmannii* (Buch. ex Magnus) Shinnery (*Zosterella longituba* E. J. Alex.) has been recognized by some (e.g., Alexander; Correll & Correll) as being distinct from *H. dubia* (Jacq.) MacM. (*Zosterella dubia* (Jacq.) Small) because of differences in flower size and seed morphology. The perianth tubes of *H. Liebmannii* are usually much longer than those of *H. dubia* (5–12 vs. 1.5–7 cm), and the seeds of the former are nearly globose, black-brown, and 14- to 16-ribbed, while those of the latter are ellipsoid, yellow-brown, and 10- to 12-ribbed. Horn has reported, however, that from north to south there is a general increase in perianth-tube length and that, although there is a genetic component, shorter perianth tubes were produced on cooler mornings among experimental plants. He also found that seed color was related to development and that the number of ribs per seed varied within populations.

Heteranthera dubia occurs at various depths and tolerates a relatively wide range of temperatures (Steyermark) in still to swift, usually alkaline water (Hellquist & Crow; Muenscher, 1944; De Wit). The species is known from southern Quebec to North Dakota, south to Texas and Florida, and from more scattered localities in Washington, Oregon, California, Arizona, Mexico, Cen-

tral America, and the Caribbean region. *Heteranthera Liebmannii* is found on mud or in relatively still water from Alabama to Mexico and the Caribbean (i.e., it has a more southern distribution than *H. dubia*) and is reportedly more abundant than *H. dubia* in Texas (Correll & Correll).

Horn (1983) determined that mature seeds of *Heteranthera dubia* sink upon being released in autumn and germinate the following spring. Plants flower in the first year and may overwinter *in toto* beneath the ice, although growth does not occur below 8°C. In shallow and/or swift water the plants may produce much shorter stems and internodes, forming denser, more circular patches (Steyermark) that may provide food and shelter for fish (Correll & Correll). Plants growing on mud develop short, stiff leaves and stems and have been recognized under various names (see Horn, 1983). Although such variants have been considered to be environmentally induced and therefore unworthy of formal taxonomic recognition (Horn, 1983; Steyermark), it is interesting and possibly significant that they are more likely to flower than those in more typical, aquatic conditions (Fassett). While emersed plants flower to some extent, most submersed ones are sterile or develop only flowers that are hidden in the leaf axils and do not open (Voss, under family references). Thieret reported that such flowers are structurally identical to chasmogamous ones and showed that they were induced when buds did not reach the surface or when they were pulled under water by the current.

Flower color, which is variable in *Heteranthera*, has been described in detail by Horn (1985a). Among species of subg. HETERANTHERA in our area, the basic perianth color is purple, lavender, pale blue, or white (yellow, or rarely blue or white in the extraregional *H. Seubertiana* Solms; blue or white in the extraregional *H. zosterifolia* Mart.), while the upper middle lobe is variously marked with dark purple, brown, green, and/or yellow. The central and lateral stamens, as well as the filament and anther of any one stamen, usually differ in color; either filaments or anthers are purple, blue, yellow, or white. Styles and (evidently) stigmas are either purple or white (the style is yellow and the stigma blue in *H. zosterifolia*). With the exception of purple stigmatic hairs, all externally visible flower parts of *H. dubia* (subg. ZOSTERELLA) are yellow or pale yellow.

There is some evidence that the stamen dimorphism (both in color and size) found in species of subg. HETERANTHERA is related to pollination biology. According to studies of *H. reniformis* by Lovell, pollen from the pale blue or greenish anther of the long central stamen is deposited on a visiting bee while it gathers pollen (the flowers lack nectaries) from the more conspicuous yellow anthers of the shorter lateral stamens. Such observations, including that of a green color for the central anther, evidently have not been corroborated by other workers.

The only economic significance of *Heteranthera* involves the occurrence of some of its members as weeds in rice fields: *H. reniformis* and *H. limosa* in the United States (Barrett, 1978b) and *H. reniformis* in northern Italy (Webb, in Valentine). The seeds of various species, including *H. dubia*, are eaten by wildfowl (McAtee; see also Fassett). Both *H. dubia* and *H. reniformis* are

considered to be rare and endangered in various northeastern states (Hellquist & Crow).

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Tribe PONTEDERIAEAE [Schwartz, Bot. Jahrb. **61**(Beibl. 139): 39. 1927]

3. **Pontederia** Linnaeus, Sp. Pl. **1**: 288. 1753; Gen. Pl. ed. 5. 140. 1754.

Perennial, emersed herbs. Stems stout and more or less horizontal. Adult leaves exstipulate; petiolate, petioles usually much longer than blades, not inflated; blades sagittate, cordate, ovate, or elliptic. Inflorescence a spikelike panicle,⁴ pedunculate, the subtending bract sometimes mucronate, the single leaf on each flowering-stem with a large, sheathing base and a petiole much shorter than the blade. Flowers perfect, all species tristylous except the homostylous *P. parviflora*; perianth mostly funnellform, zygomorphic, with 6 lobes in 2 lips of equal [or unequal] lobe number. Stamens 6, unequal in length; filaments straight or curved; anthers oblong, auriculate, much shorter than the filaments and somewhat movable on them, the adaxial 3 either included deep within the perianth tube or near its summit, lower than the abaxial 3, which are either near the summit of the perianth tube or exerted. Ovary with 2 abortive locules and 1 fertile one with a solitary ovule pendulous from a terminal placenta; stigma (depending on style length) included deep within the perianth tube, or near its summit, or exerted. Fruit a 1-seeded utricle enclosed in the accrescent, roughened, ridged, and terminally coiled base of the perianth tube, tipped by the coiled base of the style; seeds not ribbed. (Including *Reussia* Endl., 1836, nom. cons., and *Unisema* Raf., 1808, "*Umsema*.") TYPE SPECIES: *P. cordata* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **1**: 462. 1913, and discussion below. (Named for Giulio Pontedera, 1688–1757, professor of botany in Padua, Italy; see *Critica Botanica*, p. 94. 1737 [p. 77 in English transl. by A. Hort, 1938].)—PICKEREL-WEED, BLACK-POTATO, WAMPEE, WILD-GENTIAN.

A small New World genus of five species (Lowden), *Pontederia* is characterized by a two-lipped perianth, a one-locular ovary (through the abortion of two locules) containing a single pendulous ovule, and six stamens. The genus is, for the most part, tropical to subtropical in its distribution. The plants grow primarily in fresh inland water and in brackish rivers and marshes near the sea.

Lowden's revision of *Pontederia* incorporated evidence from chemistry (phenolics), cytology, and morphology and also included considerations of nomenclatural history, dispersal mechanisms, breeding systems, and evolutionary development. He reviewed the controversy surrounding interpretation of the Linnaean genus *Pontederia* and concluded that of the three species listed in the first edition of *Species Plantarum*, only *P. cordata* L. belonged and must therefore be considered the type. *Pontederia ovata* L., with one stamen, was clearly out of place in a genus that was included in the Linnaean class Hexandria, and the species has since been removed to the Marantaceae. The third species, *P. hastata* L. (actinomorphic perianths of mostly free parts, six stamens in

⁴The flowers are sessile and are grouped in sessile clusters along the main axis of the inflorescence; flowers along the axis, as well as within each cluster, are in various stages of development, suggesting that the clusters represent reduced branches or branch systems. At least partial resupination of most flowers is therefore suggested by their uniform orientation at anthesis. (Also see Leggett, 1875.)

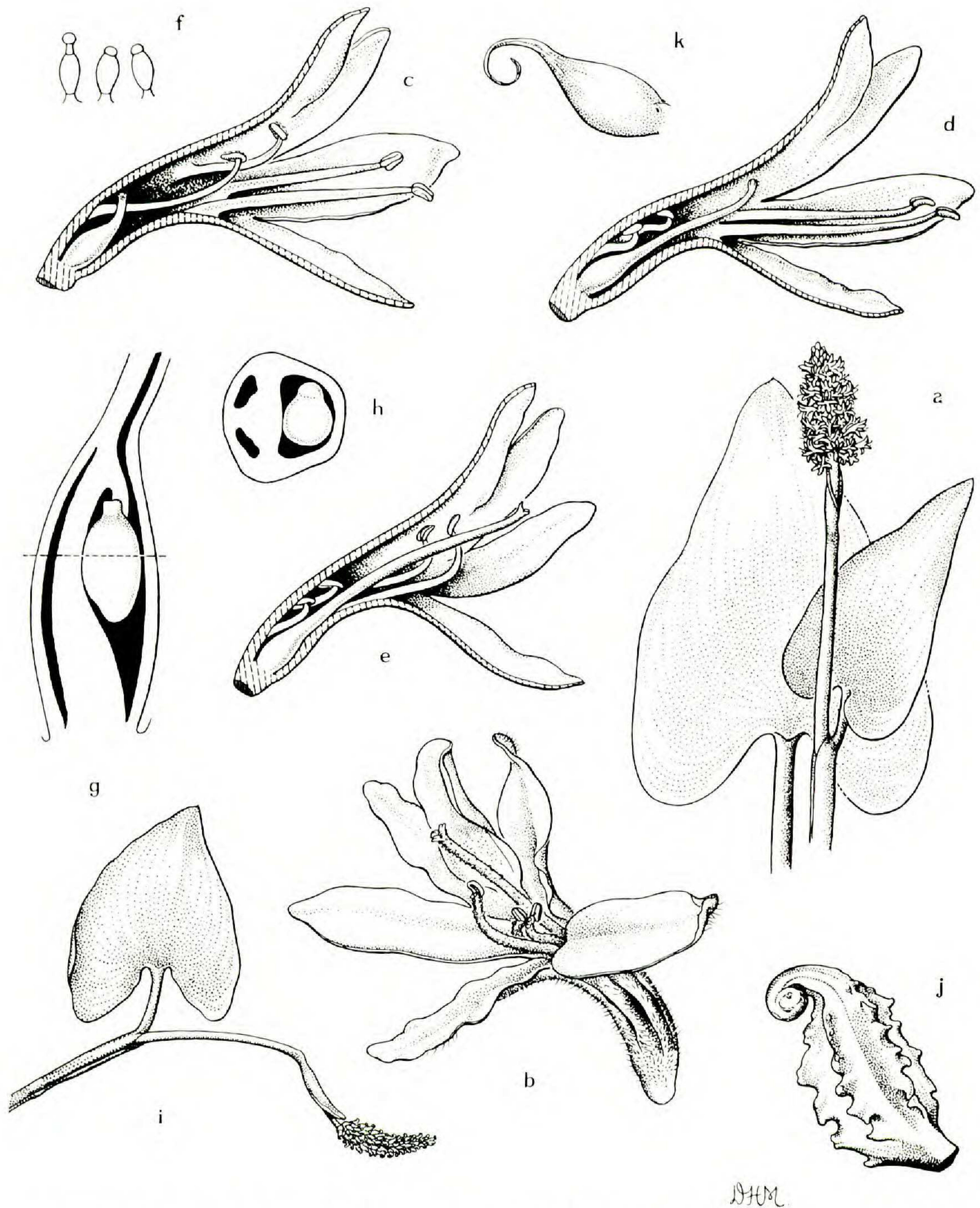


FIGURE 1. *Pontederia*. a-k, *P. cordata*: a, leaf blade and portion of petiole behind flowering stem (terminal part) with leaf and bract subtending inflorescence, $\times \frac{1}{4}$; b, flower of long-styled form, with style and 3 mid-length stamens exerted, $\times 3$; c, flower of short-styled form, in semidiagrammatic longitudinal section (e.g., hairs not shown), showing 2 of 3 adaxial, mid-length stamens and 2 of 3 abaxial, long stamens, $\times 3$; d, flower of mid-styled form (drawn as in "c"), showing 2 of 3 adaxial, short stamens and 2 of 3 abaxial, long stamens, $\times 3$; e, flower of long-styled form (as in "c"), showing 2 of 3 adaxial, short stamens and 2 of 3 abaxial, mid-length stamens, $\times 3$; f, glandular hairs of staminal filaments, $\times 50$; g, ovary, in longitudinal section, showing position of 1 aborted locule (at left) and fertile locule with its single pendulous, anatropous ovule, $\times 16$; h, ovary, in transverse section (at level of dashed line in "g"), showing 2 aborted, adaxial locules and fertile locule with its single ovule, $\times 16$; i, terminal part of flowering

groups of five and one based on length, and many seeds per fruit), has been placed by most botanists in the Old World genus *Monochoria* Presl.⁵

Lowden decided to treat *Reussia* Endl. as a subgenus of *Pontederia* because the supposed morphological differences between the two groups are weak and/or evidently unclear. According to him, the perianth in *Pontederia* clearly has two lips of three lobes each, while that in *Reussia* has an upper lip of four lobes and a lower of two by some accounts, but an upper of five and a lower of one by others. In addition, the genera are similar in other aspects of morphology, including an ovary with one fertile locule and a single pendulous ovule. Lowden reported haploid chromosome counts of $n = 8$ in subg. PONTEDERIA (ridges of the persistent, accrescent perianth base encasing the fruit smooth or toothed; flowering shoot erect) for *P. cordata* var. *cordata*, *P. parviflora* E. J. Alex., and *P. sagittata* Presl, and $n = 16$ in subg. REUSSIA (Endl.) Lowden (ridges of perianth base spinulose; flowering shoots prostrate) for *P. rotundifolia* L. f.

Chemical data provided by Lowden are consistent with the inclusion of *Reussia* as a subgenus in *Pontederia* on the basis of coefficients of similarity⁶ he calculated for all pairs of the included taxa of *Pontederia* (*P. cordata* vars. *cordata*, *lancifolia* (Muhl.) Torrey, and *ovalis* (Mart. in Roemer & Schultes) Solms in DC., *P. parviflora*, and *P. sagittata*, of subg. PONTEDERIA; *P. rotundifolia*, of subg. REUSSIA), as well as on those I calculated for all pairings involving *Heteranthera limosa*, *Eichhornia crassipes*, and the foregoing taxa of *Pontederia*. Mean values for coefficients of similarity (zero indicating no resemblance, one indicating identity) were lower between genera of Pontederiaceae (*Pontederia*-*Eichhornia*, 0.58; *Pontederia*-*Heteranthera*, 0.49; *Eichhornia*-*Heteranthera*, 0.50) than between subgenera of *Pontederia* (subg. *Pontederia*-subg. *Reussia*, 0.69), although greater between subgenera than between included taxa of subg. *Pontederia* (0.62).

Lowden speculated that *Pontederia* originated in the American tropics from tristylous, aquatic ancestors with many-flowered spikes and flowers with zygomorphic perianths of basally connate parts, six stamens, and a single pen-

⁵Rafinesque (Med. Repos. N. Y. II. 5: 532. 1808) placed *Pontederia cordata*, with a single seed per fruit, in his new genus *Unisema* ("Umsema") and retained *P. hastata*, with many seeds per fruit, in *Pontederia*, presumably because Linnaeus had used the term "capsula" in describing his genus. Lowden maintained, however, that the term had been used to describe the accrescent base of the perianth tube surrounding the fruit and did not therefore indicate a many-seeded fruit. Fernald (Rhodora 27: 76-81. 1925) pointed out that in dedicating the genus to Pontedera, Linnaeus primarily had plants from North America in mind, and that in the fifth edition of *Genera Plantarum* he added to *Pontederia* a tropical American plant with one-seeded fruits, thus strengthening the idea that his concept of *Pontederia* excluded plants with many seeds per fruit.

⁶Between any two taxa, the coefficient of similarity is the number of phenolic compounds in common divided by the sum of this number and the number of phenolics present in only one or the other.

stem during fruit maturation, which occurs under water, $\times \frac{1}{8}$; j, accrescent, terminally coiled base of perianth tube enclosing utricle, $\times 3$; k, 1-seeded utricle with persistent, coiled base of style, $\times 3$.

dulous ovule. He proposed that sometime during the Tertiary the genus spread from Central to North America, where it initially occurred farther west than it does at present. Fossils attributable to *Pontederia cordata* have been recovered from the Green River Formation in Wyoming, now considered to be early or mid-Eocene (Bradley, Knowlton).

Pontederia is represented in the Southeast by three commonly accepted but taxonomically questionable varieties of *P. cordata* (see below). The species is distinguished from others in subg. PONTEDERIA by a combination of characters, including tristyly and teeth on the ridges of the persistent, accrescent perianth bases. The plants are largely restricted to stream banks and pond edges where bare ground (required for seed germination) is exposed by fluctuating water levels; few individuals are found in "high marsh plant communities" (see Whigham & Simpson).

Variety *cordata* (leaves sagittate, cordate, reniform, or hastate; mature floral tube glabrous or sparsely glandular) occurs throughout the eastern United States and adjacent Canada but is most abundant in the Great Lakes region, in the Northeast, and on the Gulf and Atlantic coastal plains. It is also found in southern Brazil and adjacent areas, as well as in Belize, where Lowden reported specimens that suggested hybridization with *P. sagittata*. The distribution of var. *lancifolia* (*P. lancifolia* Muhl., 1813; *P. angustifolia* Pursh, 1814; *P. lanceolata* Nutt., 1818) (leaves narrowly to broadly lanceolate, mature floral tube glandular) matches that of var. *cordata*, with the exception that it appears to be rare in the Great Lakes region and otherwise less common than var. *cordata* in North America outside of southern Georgia and Florida; Lowden reported it from two localities in Cuba as well. Perry observed that var. *lancifolia* is less hardy than var. *cordata*, which perhaps explains its more southern distribution. Godfrey & Wooten reported that vars. *cordata* and *lancifolia* are not easily distinguished in Florida and southern Georgia, where each occurs in abundance, and my own observations suggest that the same is true elsewhere in the Southeast. Both varieties are popular among gardeners and have become naturalized in parts of the Old World (Aston; Casper & Krausch; Clapham *et al.*; Valentine). According to Lowden, var. *ovalis* is restricted to South America and differs from broad-leaved specimens of var. *lancifolia* in its densely pubescent upper peduncles. Nevertheless, *Mather M-277* (GH), from Marion County, Florida, was determined by Lowden to belong to var. *ovalis*. My observations indicate that the upper peduncles of many specimens of var. *lancifolia* from our area are as densely pubescent as those of this specimen.

The two subgenera of *Pontederia* differ in the relative importance of vegetative and sexual reproduction (Lowden). In subg. REUSSIA, members of which have few-flowered inflorescences and long, trailing stems, reproduction through fragmentation of adventitiously rooted stems has a greater immediate value than reproduction by seeds, especially in populations composed of a single floral form (in which all pollinations would be illegitimate and thwarted by physiological incompatibility systems). In contrast, sexual reproduction may be of greater importance in subg. PONTEDERIA because inflorescences are many flowered and the stems are more erect, above ground, and shorter.

All species of *Pontederia* are tristylous, with the exception of *P. parviflora*

(subg. PONTEDERIA), in which homostyly (semihomostyly according to Barrett, 1979) is thought to have been derived from the tristylous condition (Lowden). Ornduff studied the breeding system of *P. cordata* in a number of populations along the Atlantic Coastal Plain in the Southeast. Except for one population in North Carolina in which only short- and mid-styled flowers occurred, all three floral morphs were represented in each population. Populations varied, however, in the relative proportions of each morph, presumably because of a combination of founder effects and vegetative reproduction (see, however, Price & Barrett, 1982).

Although data regarding the genetic basis for tristily in the diploid *Pontederia cordata* are not yet completely available, Barrett, Price, & Shore assumed it was the same as that observed in the diploid *Eichhornia paniculata*, in which two alleles are present at each of two loci, one of which is epistatic to the other. Essentially the same is true of *E. crassipes*, except that this species is a tetraploid (see also Barrett, 1985a [under *Eichhornia*], Charlesworth; see, however, Barrett & Anderson).

In *Pontederia cordata*, as in the majority of other tristylous plants investigated, legitimate pollinations are most effective in producing seed. Illegitimate pollinations are less productive both because they are less frequent and because of the existence of a physiological incompatibility system. Ornduff provided data from artificial pollinations indicating that in *P. cordata* the incompatibility is due to "carpellary factors" (i.e., is of the sporophytic type) and is strongest in the short-styled form, slightly weaker in the long-styled, and clearly weakest in the mid-styled (see also Barrett *et al.*). Barrett & Anderson summarized data from *P. cordata* vars. *cordata* and *lancifolia*, *P. rotundifolia*, and *P. sagittata* showing that in each the level of self-compatibility, as determined by percentage of seed set in flowers pollinated with the most compatible pollen (i.e., that from short, medium, or long stamens), is clearly and consistently greatest in the mid-styled form, with the exception that seed set in the long-styled form of *P. rotundifolia* is approximately equal to that of its mid-styled form. These data also suggest that the relationships between self-compatibility levels in the short- and long-styled forms are rather inconsistent among the four taxa. Barrett & Anderson proposed several hypotheses to explain their observations.

Price & Barrett (1982) investigated tristily in 74 North American populations of *Pontederia cordata*, including 45 from the Southeast, and for the most part substantiated the findings of Ornduff. They also determined, however, that the mid-level (medium) stamens of short-styled flowers produced about twice as many pollen grains as those of long-styled ones. Although the basis of this difference could not be established, Barrett, Price, & Shore later suggested that it could result from differences in the time of anther development, since the mid-level stamens of the short-styled morph are the lower set, while those of the long-styled morph are the upper set (i.e., the lower set of anthers develops first, so these are therefore larger and more productive of pollen). Price & Barrett (1982) also suggested that pollen from short-styled flowers fertilizes more ovules of the mid-styled morph than does pollen from the long-styled morph (although Barrett, Price, & Shore later reported that field studies provided only limited evidence that this was so) and that this difference may

influence the composition of natural populations in favor of the short-styled form.

On the basis of data gathered from the same 74 populations mentioned above, Barrett, Price, & Shore reported that of 69 trimorphic populations, 76.8 percent were significantly anisoplethic (although morph frequencies varied among populations, presumably because most had not yet reached equilibrium). Most frequently encountered were a predominance of the short-styled morph and a deficiency of the long-styled one, regardless of variety (var. *cordata* or var. *lancifolia*), habitat type (permanent or temporary), locality (Ontario and Wisconsin or the Carolinas, Georgia, Florida, and Louisiana), population size (more or fewer than 500 inflorescences), location within a population (divided into 10 × 2 m sections), or time (populations observed for five years). Because of the large sample of populations employed, they considered it unlikely that historical factors (e.g., dispersal, disturbance, establishment) alone could be responsible for the anisoplethy observed in *Pontederia cordata*; they proposed instead the existence of some selective advantage for the short-styled morph and a corresponding disadvantage for the long-styled one. It is interesting that Price & Barrett (1984) reported that legitimate pollinations were most frequent in the long-styled morph, followed in order by the mid- and short-styled morphs, possibly due at least in part to differences in amount of surface area available for pollen deposition (e.g., the pollinator's proboscis tip, which normally delivers pollen to short styles, is smaller than its head, which delivers to mid-length styles). Nevertheless, Price & Barrett (1982) reported no statistically significant differences among floral morphs in flowering phenology, fruit weight, germination percentage, number of inflorescences per individual, or flowers (all or chasmogamous only) and seeds per inflorescence. It is notable that while the situation in *P. sagittata* appears to be almost identical to that in *P. cordata*, it is considerably different in *Eichhornia* (see discussion of that genus).

Perianths in species of *Pontederia* (including *P. cordata* as represented in the Southeast) are purple, blue-purple, blue, pale blue, or white, and the anthers are blue. The extraregional *P. subovata* (Seub. in Mart.) Lowden differs from this pattern in sometimes having blue-green perianths, while *P. parviflora* (the only homostylous species of *Pontederia*, see above) has greenish white to white perianths and black to brown anthers (Lowden). The upper-middle perianth lobe in species of *Pontederia* bears a single bilobed yellow spot (Lowden) or two separate yellow spots (Lovell).

The flowers of *Pontederia cordata* attract a number of insect visitors, primarily bees of the genera *Bombus*, *Melissodes*, and *Xylocopa* (Price & Barrett, 1982, 1984). The emergence of *Dufourea novaeangliae* (Robertson), a small solitary bee, coincides remarkably well with the onset of flowering in *P. cordata*, and the insect is not known to visit any of the many other species concurrently available (Lovell, Percival; see, however, Hurd). According to Hazen, the numerous insects that visit *P. cordata* do so primarily for nectar, which is produced by three septal nectaries, but some hymenopterans also collect pollen. Price & Barrett (1982) determined that the frequency of visits to *P. cordata* by bum-

bees (*Bombus* spp.) in a Canadian (Ontario) population was independent of floral form.

Evidence provided by Price & Barrett (1984) suggests that the frequency of legitimate pollinations in populations of *Pontederia cordata* may be dependent on the type of pollinators involved and may therefore vary geographically. In northern North America, species of *Bombus*, which have broad preferences and are therefore probably not highly co-adapted to the breeding system of *P. cordata*, are the most important pollinators. In the South, on the other hand, a diverse set of more specific (long-tongued) pollinators is involved, perhaps most importantly species of *Melissodes*. These observations may help to explain why significant levels of legitimate pollination (i.e., levels significantly greater than those predicted by a model that assumes random pollination) appear to become less frequent with increasing latitude in the species as a whole. In Florida, populations of all three morphs experienced significant levels of legitimate pollination, in the Carolinas only some did, and in Ontario none did.

The fruits and associated perianth bases of *Pontederia* are buoyant because of the presence of aerenchyma in the latter and normally float for more than 15 days, according to Schulz. Transport by water is considered to be the primary means of dispersal. Dissemination by ducks and other animals is less important and probably involves only relatively short distances (see Sculthorpe). *Pontederia cordata* has been recorded as a food source for the southern black or mottled duck (*Anas fulvigula*), and the seeds have been found in the stomachs of wood ducks (*Aix sponsa*) (Ridley). Lowden observed that the spinulose perianth bases encasing the fruits of *P. rotundifolia* become attached to livestock in El Salvador and Costa Rica, but in subg. PONTEDERIA (including our plants) such surfaces are smooth or only toothed, and the fruits are probably less effectively dispersed in this way.

Pontederia cordata is widely grown as an aquatic ornamental, and it sometimes escapes cultivation. It is reportedly naturalized in Britain (Clapham *et al.*) and southern Europe (Valentine). In South America and perhaps elsewhere it frequently occurs as a weed in rice fields (Barrett, 1978b).

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Note added in proof. Since this treatment was completed, a paper of considerable significance has appeared in the literature. Various cladistic analyses reported by Eckenwalder & Barrett (under family references; annotation based on a manuscript copy of the abstract) suggested that the Pontederiaceae and Philydraceae are sister groups and that the former is divisible into two groups of two genera each. *Pontederia* (including *Reussia* as a subgenus) and *Eichhornia* were depicted as one clade, while *Heteranthera* (including *Eurystemon*, *Hydrothrix*, *Scholleropsis*, and *Zosterella*) and *Monochoria* comprised the other. The family, the two clades, three of the four genera, and both subgenera were considered to be monophyletic, while *Eichhornia* was said to be paraphyletic. The cladograms generally indicated that tristyly is not the primitive breeding system in the Pontederiaceae and that it did not arise more than once in the family. Although it was shown to be a synapomorphy of the *Pontederia-Eichhornia* clade, its evolutionary relationship to homostyly in *Eichhornia* was not resolved. The possibility that the dimorphic stamens of the *Heteranthera-Monochoria* clade were not derived from a tristylous condition was also suggested. A base chromosome number of $n = 8$ for the family was favored, from which $n = 7$ and $n = 15$ would have been repeatedly derived. The cytological diversity in the family was thought to have resulted from both aneuploidy and polyploidy.—T. J. R.